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THE SKULL AND EXTREMITIES OF DIPLOCAULUS.

By S. W. WILLISTON, University of Chicago, Chicago, Ill.

IN 1877[1] Professor Cope described, from the reputed Permian of Texas, some small vertebræ as of a salamander-like reptile under the name *Diplocaulus salamandroides*. The type specimens, now in the possession of the University of Chicago, were later figured by Case.[2] In 1882 Cope[3] recognized the same genus from the Permian of Texas, and described more fully a species of a much larger size under the name *D. magnicornis*, which he now referred to the Microsauria and to the family Diplocaulidæ, which he had previously proposed in a catalogue of the Permian vertebrates as a member of the Pelycosauria.[4] He here describes for the first time the characteristic zygosphene. In 1895 Cope,[5] with better material of *D. magnicornis*, gave a more complete description, correctly figuring the upper surface of the skull and the anterior part of the palate. He also described here briefly a third species of the genus as *D. limbatus*, also from the Texas Permian, and characterized chiefly by the posterior concavity of the cranium and the greater protuberance of the quadratojugal posteriorly.

In 1902 Broili[6] published a preliminary description, with a rather poor figure, of the same species, giving for the first time the nearly complete structure of the palatal region. In the following year Jaekel[7] reproduced these figures and made some additional observations in a discussion of *Diceratosaurus*. Again, in 1904 Broili[8] published a more complete description of the same form, with additional figures, and referred the genus to a new family, the Diplocaulidæ, under the misapprehension that Cope's name, given in error of the real relationships of the animal, had become obsolete. In this latter paper Broili also described and named two additional species, *D. copei* and *D. pusillus*, the latter a very small species, and doubtfully, I think, belonging in this genus.

During the past year an expedition to the Permian of Texas from the University of Chicago secured a number of excellent specimens of *Diplocaulus* of what appear to be distinctly two species, together with a large quantity of more or less intermingled remains of two additional smaller species of the genus from the Permian bone-bed near Orlando, Okla. This material enables me to determine much that is new and of interest concerning this singular genus of paleozoic amphibians, not the least of which is the discovery of small but well-formed limbs, both anterior and posterior, which had been previously never detected in the abundant material known. There is yet much to be learned concerning the structure and especially the habits of these remarkable animals; so much that I do not venture to give a restoration of the creature. The figures, carefully drawn by myself, will render unnecessary a detailed description of the bones.

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[1] Proc. Amer. Phil. Soc., 1877, p. 187.

[2] Journal of Geology, 1900, p. 710, pl. I, ff. 16*a*–17*b*; pl. V, ff. 17*a*–17*d*.

[3] Proc. Amer. Phil. Soc., 1882, p. 451.

[4] American Naturalist, XV, 1881, p. 162.

[5] Proc. Amer. Phil. Soc., 1895, p. 455, pl. IX.

[6] Centralblatt f. Mineralogie.

[7] Jahresbericht f. Mineralogie, 1903.

[8] Paleontographica, LI, 1904, pl. IV, ff. 4–15; pl. V, ff. 1–4; *D. copei*, p. 21, pl. III, ff. 1, 2; *D. pusillus*, p. 24, pl. VI, ff. 1–4.

SKULL.

Two excellent skulls, both nearly complete, were obtained of two distinct forms. The better one of these two (No. 651) is perhaps the best of the genus hitherto obtained. It was found by myself lying exposed upon the top and side of a small mound, near the Wichita river, just west of the Vernon road in Texas. It was in two larger and two smaller pieces, the largest with its dorsal surface uppermost, from which the thin outer tablet of bone had been eroded by the weather, rendering the sutures for the most part very conspicuous. That I might not be biased by Cope's determinations of the sutures, I traced them quite independently, as they are reproduced in the drawings (figs. 1 and 4). A comparison with Cope's figures (reference to which will be found in the foot-note) will show how closely they agree throughout. Broili,[9] in his studies of the skull, was unable to distinguish the sutures, and even cast doubt upon Cope's determinations. With the aid of a hand lens I find no difficulty in distinguishing them in any specimen.

The figures will show sufficiently well the form and relations of the different elements to render unnecessary a detailed description of them. The absence of a distinct lachrymal bone is not at all remarkable, since other early forms either lack this element or have it excluded from the orbit; and these facts seem to support the contention of Jaekel that the element usually so-called is not really the lachrymal of the mammals, which should rather be homologized with the prefrontal, a very constant bone. The fusion of the postorbital and postfrontal is, however, unexpected. That

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9. Paleontographica, LI, p. 8, 1904. He says, after an examination of the skull figured by Cope: "auf welchem samtliche Nahte eingetragen sind, so sind dieselben in Wirklichkeit auf dem Stucke zumeist nicht vorhanden, sondern mit Farbe eingezeichnet; an einzelnen Stellen durften ja Teile von Nahten existierin, doch war es mir nich moglich infolge der eingetragenen Linien etwelche zu constatieren."

one or the other is absent in so many of the later reptiles may perhaps explain its absence here.

The maxilla presents but a very small surface on the superior aspect of the skull; on the side the suture separating it from the jugal turns backward obliquely, as shown in fig. 1, to the hind end of the dental series, passing inward obliquely to the palatines, separating apparently a transverse element, which is known to occur in other stegocephs. The parietal is very large, articulating posteriorly with the supraoccipital plates and the epiotics.

The "supraoccipitals" are clearly distinguished, both upon the upper and the under sides, articulating normally with the parietal, epiotics and exoccipitals. On the under side the suture separating them from the parietals passes inward so as to include the union with the exoccipitals. There seems to be little doubt but that these elements are real membrane bones, but they functionally subserve the same purpose as the unpaired supraoccipital of the higher animals, since there is no indication here of an intervening element between them and the occipitals. Most characteristic of the genus and family are the greatly enlarged "epiotics," produced, as they are, into such extraordinary horns. In the present species these horns are obliquely concave distally, almost spoon-like and somewhat dilated, very different from the conical termination of another skull from Texas which I must refer to *D. magnicornis*, as also from the horns of one of the small species from the Orlando bonebeds.

This modification of the extremity seems to imply a distinct functional use; very probably, as has been suggested, for the protection of the branchiæ. In the earlier amphibians the lateral cornua may be composed either of this element or of the prosquamosal (or supratemporal); in the the latter case the otic notch between the two. In reality, the same notch is found in *Diplocaulus* between the epiotic and the prosquamosal on the lateral aspect of the skull. As regards the homologies of the two elements called here the squamosal and prosquamosal there has been, as is well known, much contention. Cope called these bones in *Diplocaulus* the supramastoid and supratemporal. The more usual nomenclature is the squamosal and supratemporal, but indifferently applied. That they agree well in position and relations with the corresponding elements of the Microsauria is apparent, and I shall continue to call them, after Baur, the squamosal and prosquamosal until the problem of their homologies is more satisfactorily settled than is at present the case. The squamosal (SQ) is a small bone, articulating with the parietal, jugal, postorbital and prosquamosal. The prosquamosal (PSQ), on the other hand, is a very large bone, articulating with the epiotic, parietal, squamosal and jugal above, the quadrate and the quadratojugal below; and these seem to be the relations of the other Permian air-breathers.

The quadratojugal, or "postquadrate bone," as Cope has sometimes called it, is in reality not at all postquadrate. It unites in front with the jugal above, behind with the prosquamosal and apparently with the proximal end of the quadrate. In most specimens by pressure it is turned inward so that its chief face lies horizontal; in life, however, it was evidently directed more downward, forming by its frontal free border the margin of the fossa into which the coronoid process of the mandible fitted. A view of the left side of the specimen under discussion is shown in figure 3, but I cannot be sure that the fossa and foramen are natural. On the opposite side the fossa is less evident. In figure 3 I give a cross-section of the side opposite to the one shown at a place corresponding to the arrow mark. There is a striking difference in the relations of the bone posteriorly in this specimen from those seen in another remarkably good specimen, which must be determined as of *D. magnicornis*, in the deep notch between the protuberant end of the quadratojugal and the prosquamosal above, the so-called epiotic notch of the earlier microsaurs. It was this character which Cope laid stress upon as distinguishing his species, *D. limbatus*. That the distal termination of the horn in this specimen is a specific character seems hardly to be doubted. For the present, therefore, I call the present specimen *D. limbatus*, though the concavity of the posterior margin of the skull is quite like that of specimens referred to *D. magnicornis*.

The structure of the palatal region in this specimen has been made out quite satisfactorily, save that most of the distinguishing sutures are uncertain. The shape and arrangement of the parts agree well in general with the figures given by Cope and Broili, and there is not much to add to their descriptions. The transverse bones are clearly separated by suture from the maxilla and palatines. The quadrate seems to be free from the quadratojugals save at the proximal end; it passes upward and backward, to be attached on the under side of the posterior part of the prosquamosal. The exoccipitals pass outward a little in advance of the condyles as a long, narrow process on each side, doubtless the confluent opisthotic as far as the epiotics, uniting, for the most part, with the parietals. Between these processes and the parietals and supraoccipitals above there is a small canal or foramen leading forward into the brain cavity. Near the proximal end of the process there is also a foramen, for the vagus.

The mandible is wholly concealed from view above, articulating posteriorly by an hour-glass-shaped concavity with the quadrate. A differentiation of its elements I have not yet been able to make out, though I have a half dozen or more specimens in good preservation before me. At the anterior end of the mandible there is a second row of five small teeth, parallel with the outer or marginal row and situated close to the inner border.

VERTEBRÆ.

	mm.
Length of atlas	20
Greatest expanse of same	32
Length of second vertebra	11
Expanse of transverse processes	46
Length of third vertebra	13
Expanse	48
Length of fourth vertebra	14
Expanse	50
Length of fifth vertebra	17
Expanse	48
Length of sixth vertebra	20
Expanse	48
Length of seventh vertebra	21
Expanse	46

The atlas and the second vertebra are occasionally coössified, and Cope has mentioned the fact. Usually, however, they are separate, as is evidenced by six well-preserved specimens of the atlas before me. The figures (1, 4), together with Cope's description, will suffice. The first ribs are borne upon the second vertebra, the so-called axis; they are rather short and distally expanded. The fourth or fifth ribs, however, are slender, elongate, gently curved and not at all expanded distally. The second vertebra is much shorter than the median dorsal ones, the third, fourth and fifth increasing in length, until the full length is attained in the sixth or seventh. The transverse processes are stout and long, directed somewhat obliquely backward, the upper one, or diapophysis, arising from the arch, the lower, or parapophysis, from the centrum. The specimens figured (figs. 1, 4) are shorter and more transverse. They do not seem to be mutilations, though such is possibly the case. The arches have no real spines — merely a low obtuse ridge, especially characterized by an oval or cordiform pit posteriorly; that of the second vertebra is very large, while that of the third is either small or wanting. The zygapophysial surfaces are broad and flat and are nearly in a transverse line. The zygosphenes, a remarkable peculiarity characteristic of this genus, and in a lesser degree of *Crossotelos*, are well developed, though the surfaces are much smaller than the zygopophysial ones. The peculiar linear striations, quite characteristic of the genus, are visible on all parts of the vertebra, though less pronounced on the transverse processes.

EXTREMITIES.

It is somewhat remarkable that evidence of the appendicular skeleton has hitherto never been furnished by the numerous specimens of *Diplocaulus* which have come to light from Texas, Illinois and Oklahoma. It has, in consequence, generally been assumed that the creatures were legless and snake-like in shape and wholly adapted for aquatic life. Jaekel several years ago suggested the presence of limbs in *Diplocaulus*, because of the well-developed clavicular girdle, evidence of which was presented by Broili. That *Diplocaulus* did have limbs, both anterior and posterior ones, albeit reduced, is now abundantly demonstrated by the material collected the past season in Texas and Oklahoma for the University of Chicago. Among this material there are one complete coracoid, five humeri, seven femora, numerous ends of epipodial bones and four associated metapodials. The mesopodials were doubtless unossified.

It is a well-known fact that specimens of land vertebrates in the Texas Permian are apt to be more or less intermingled, and the association of limb bones, especially when isolated, is by no means positive proof that there was an anatomical association in life. When the fauna of the Texas beds is sufficiently well known to eliminate in large part the known from the unknown, the detection of such accidental intrusions will be a much easier matter than it is at present. Many specimens are found exposed and weathered and more or less broken; in the collection of such upon the slopes and in the gullies it may often happen that fragments from different horizons are found intermingled; in other cases bones of different individuals may actually be associated in the same matrix. In the present case the association of the limb bones with the various specimens is such as to convince the most skeptical of their anatomical relationships. The material of *Diplocaulus* at present in the University collections is as follows :

Specimen No. 610. Skull nearly complete — the nasal extremity, the extremities of the horns, and much of the palate missing; fourteen probably consecutive vertebræ, including the axis and atlas; fragments of the clavicular girdle. E. C. Case, collector, Texas.

Specimen No. 650. Skull nearly complete; one dorsal vertebra; two posterior vertebræ; femur nearly complete and extremity of metapodial. Of large size, the femur the largest of the collection. P. C. Miller, collector, Texas.

Specimen No. 651. Twenty-five vertebræ from different parts of the column, but no cervicals. Right and left femora, several extremities of epipodials; four united metapodials. Of small size, the femora the smallest of the Texas specimens. P. C. Miller, collector, Texas.

Specimen No. 652. Complete skull; twenty vertebræ, mostly continuous from the skull, a few caudals, left coracoid attached in position to the upper side of the complete clavicular girdle, as figured; right and left humeri, the right one attached in position to the under side of the cranial horn opposite the fifth vertebra; distal extremity of femur. S. W. Williston, collector, Indian creek, near the Wichita, Texas.

In addition, large quantities of more or less broken bones belonging to at least two small species from the bone-bed near Orlando, Okla. Associated with this material, and in nearly every case in immediate connection with Diplocaulus vertebræ in the matrix, several humeri, femora and ends of epipodials; none of the limb bones matrically associated with bones of other forms.

The above evidence would seem sufficient to satisfy the most hypercritical. The remarkable fact is that nearly every specimen observed the past season presented evidence of the extremities. The limb bones, so far as known, indicate small extremities, relatively quite small in proportion to the skull, or even to the vertebræ; they could hardly have been of much use in terrestrial locomotion. That the anterior limbs were attached quite close to the head will be evident from the position of the humerus, as shown in figure 2; in this specimen the vertebræ were curved closely to the side of the horn, more so than is shown in the drawing.

A nearly complete coracoid was found imbedded on the upper, visceral side of the interclavicle, and is yet firmly attached to the bone. Its position is such, immediately back of the clavicle, with the articular surface for the humerus nearly flush with the left margin of the interclavicle, that there would seem to be no doubt of its natural position. It is a thin bone, nearly regularly oval in shape, save for the thickened emargination on the outer posterior part, for the reception of the humerus. A small foramen is visible on the

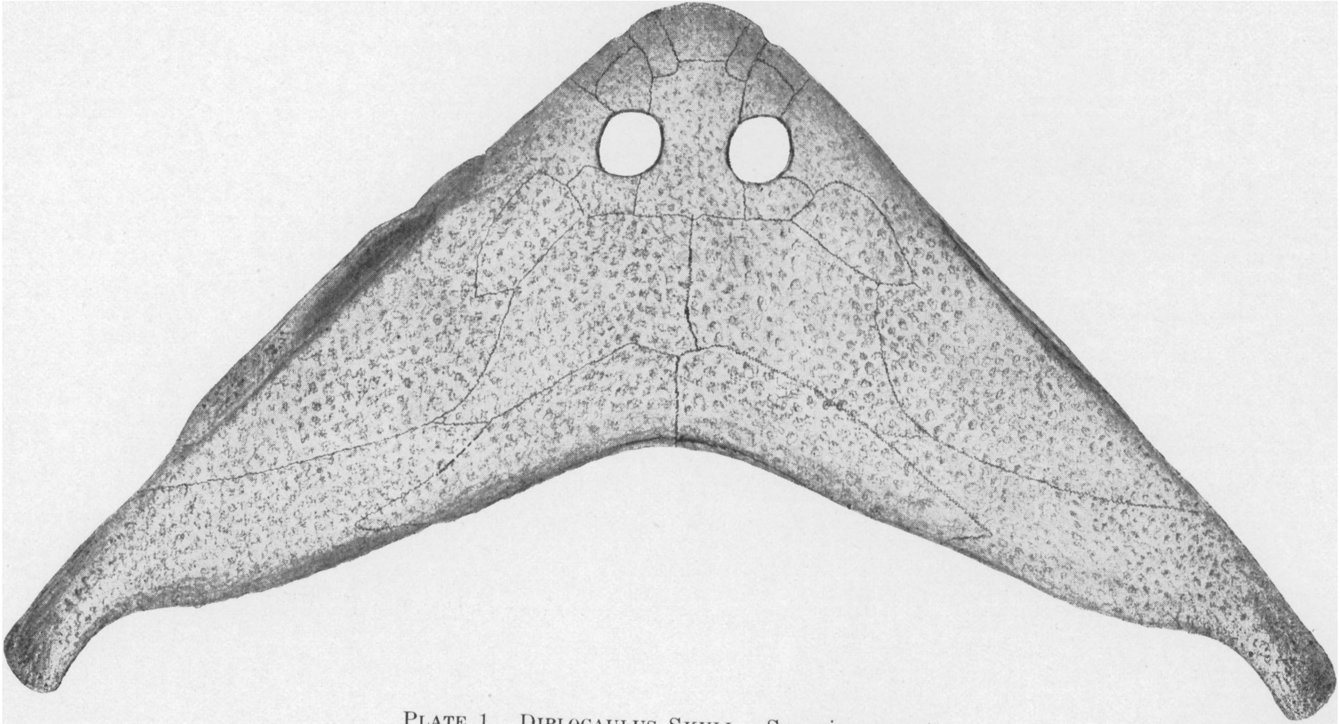

PLATE 1. DIPLOCAULUS SKULL. Superior aspect.

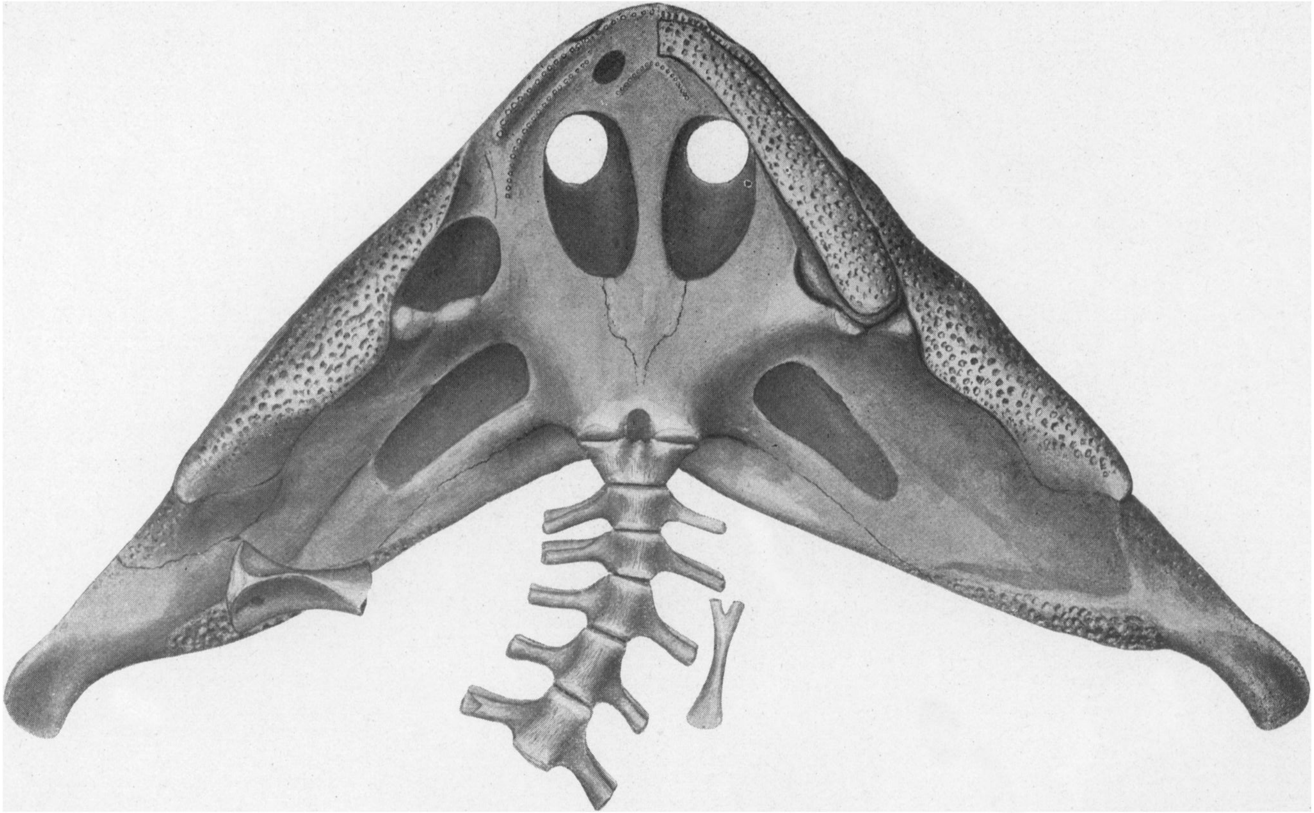

PLATE 2. DIPLOCAULUS SKULL. From below, with vertebræ and coracoid.

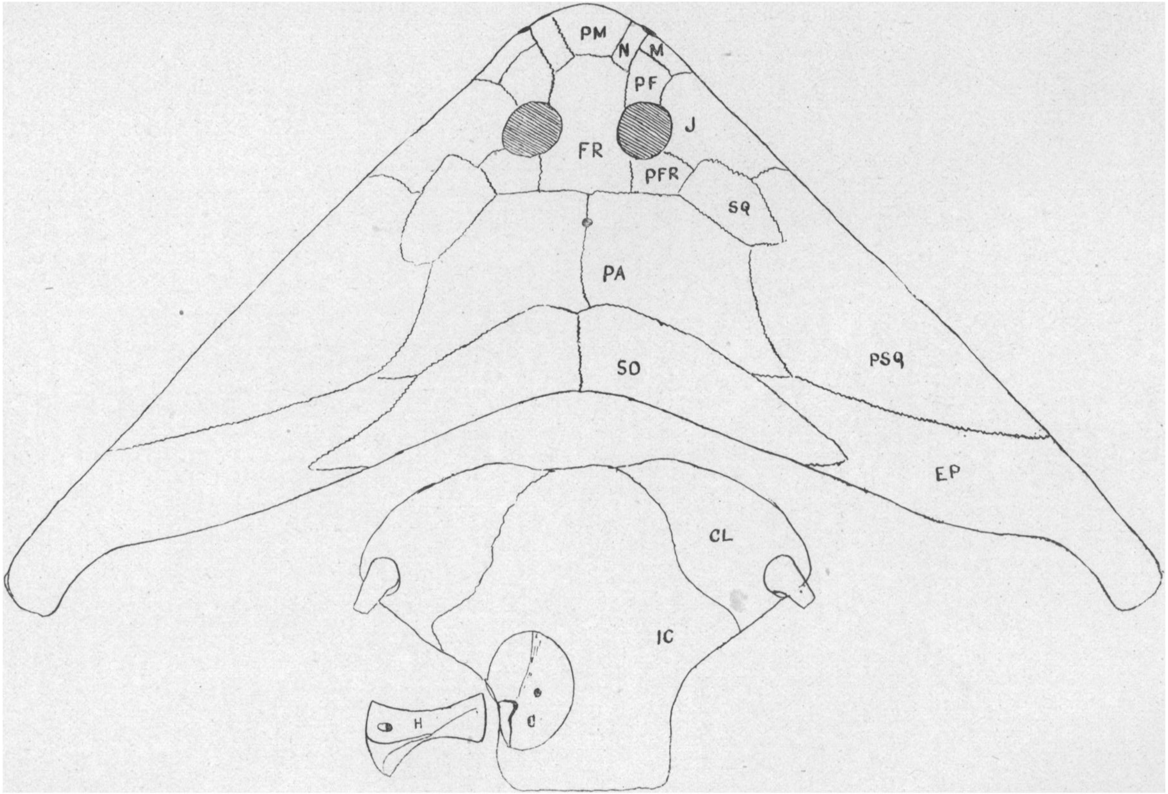

Plate 1*a*. Sutures of skull. Plate 4*a*. Clavicular girdle.

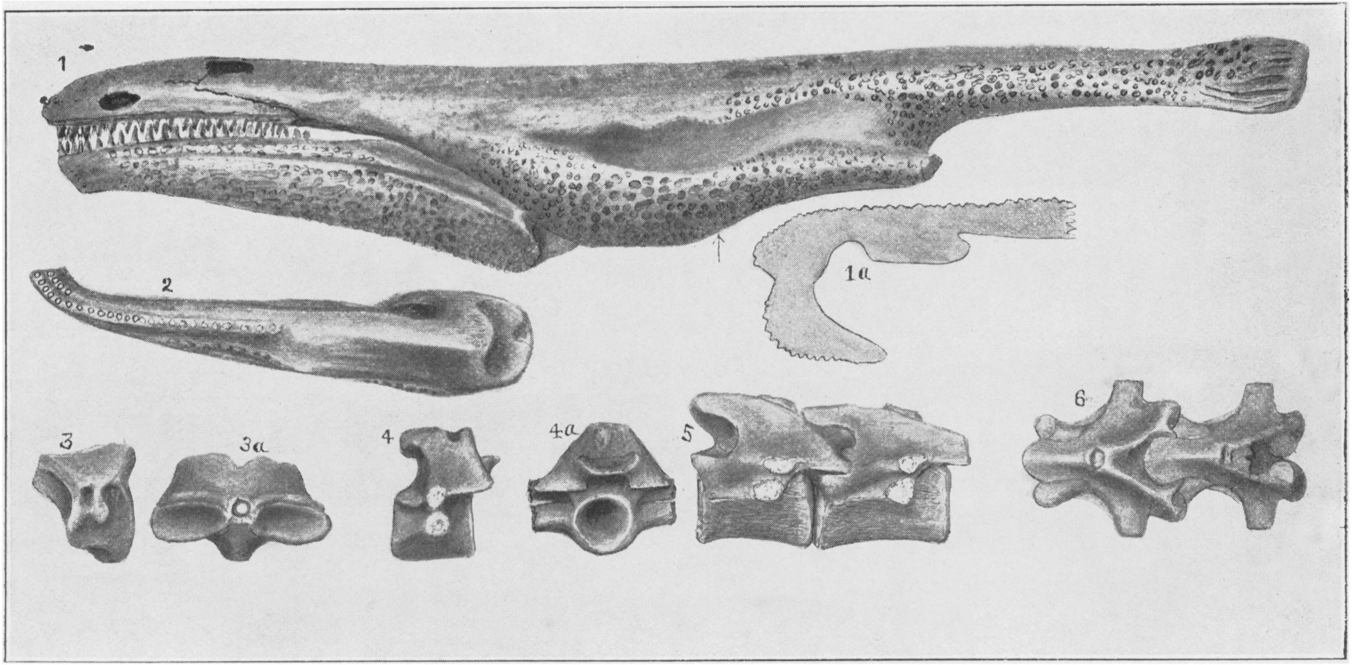

PLATE 3. **DIPLOCAULUS.** Side view, with small bones.

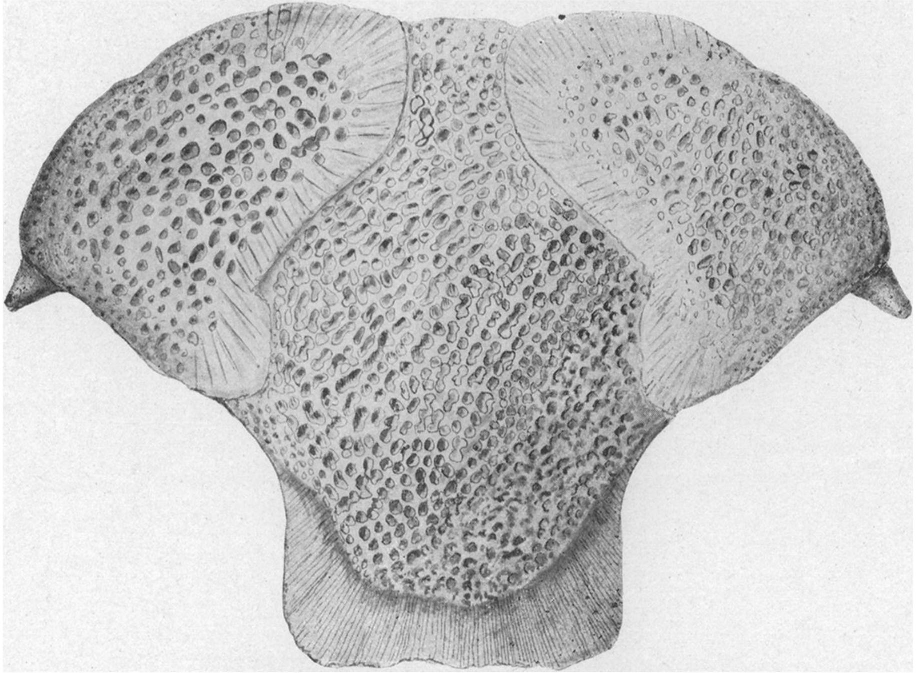

PLATE 4. DIPLOCAULUS. Clavicular girdle.

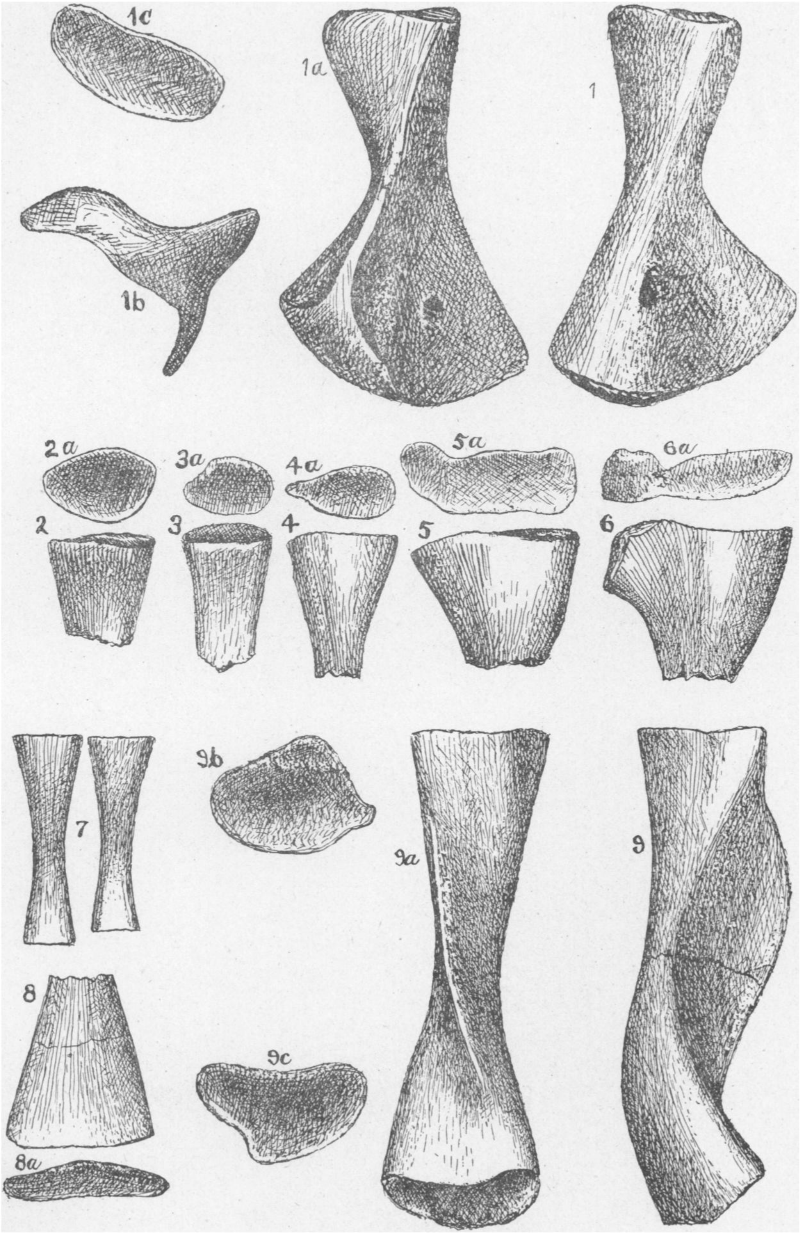

PLATE 5. DIPLOCAULUS. Limb bones.

FIG. 1. Humerus, dorsal view; 1*a*, the same, ventral view; 1*b*, proximal articulate; 1*d*, distal articulate.

FIGS. 2 to 6, epipodials; 2*a* to 6*a*, articulates.

FIG. 7. Metapodials; 8, 8*a*, epipodial; 9, femur, external view; 9*a*, posterior view; 9*b*, proximal articulate; 9*c*, distal articulate.

inner side back of the middle and not far from the margin. Because of this position and absence of any distinct sutures, I believe that the bone is the coracoid only, and that the scapula was a separately ossified bone. An outline of the bone in its relative size is shown in plate 2.

The clavicular girdle, found with its parts in nearly perfect relations, the outer side of the right clavicle only missing, is remarkable for its large size. The three bones together form a gently concave trough, nearly straight in the middle antero-posteriorly. All the bones show on their outer surface the characteristic pitting of the skull, with their margins thinned and delicately grooved radially. A stout process from the clavicle on each side is directed inward and upward, and somewhat backward, perhaps for attachment to the yet undiscovered scapula. A figure of the united bones from below is shown in plate 2; and the outline of the three with the attached coracoid in plate 4. The rather stout humerus has its two extremities twisted at an angle of about forty-five degrees. The proximal extremity (plate 3) is transversely expanded and of moderate thickness, without tuberosity of any kind; indeed until the discovery of the epicondylar foramen I was disposed to consider this the distal extremity, though rather puzzled to account for the transposition of the right humerus attached to the skull apparently in immediate connection with the pectoral girdle. The distal extremity has a much greater expansion and thickening. Distally and laterally there is a well-defined canal piercing the bone obliquely, evidence for which is corroborated in other specimens from Orlando. The presence of an epicondylar foramen has usually been considered as characteristic of the reptiles and wanting in the amphibians, though Cope expressly mentions such a foramen in *Acheloma*, a Texas temnospondyle. From the opposite side a narrow but high ridge ascends the bone obliquely about half way toward the opposite side, extending nearly to the extremity as an elevated ridge. The shape of the bone in different aspects will be well understood by reference to the figures made from a well-preserved specimen of small size from the Orlando beds.

Of the femora the best preserved is one from specimen No. 651; various others from Texas and Orlando agree well with it. The bone is much more slender than the humerus, with the proximal and distal expansions subequal and but moderate in extent. On the posterior side there is a high but thin oblique crest, occupying about three-fifths the length of the bone, and reaching neither extremity. The bone distally is curved strongly backward, so that its articular surface looks backward at an angle of about twenty degrees. So far I have found no complete epipodial bone, though doubtless a careful search of the Orlando material will reveal such. The extremities of a number of epipodials are shown in the figures (pl. 3). They are parts of the tibia and fibula. Associated with No. 651 are four metapodials attached and lying parallel, or nearly so, in the matrix. They are simple bones, as one would expect, with the shaft moderately constricted, the extremities truncate. It is very evident that the hind extremities were more slender than the anterior ones, and probably longer, preserving more of the terrestrial characters, and doubtless also of use upon land. Nevertheless their size, in comparison with that of the vertebræ, is small.

In none of the Texas material at command is there any evidence whatever of dermal ossifications, other than the clavicular gridle. Nor do I find any certain evidence of such from the Orlando material. Dermal plates are there in abundance in this material, but none intimately associated with *Diplocaulus* bones; whereas specimens of *Crossotelos*, another form which must for the present be located with *Diplocaulus* among the Microsauria, though aberrant, show abundant evidence of ventral ribs and probably also dermal scutes. All of which goes to show that *Diplocaulus* was a bare-skinned amphibian of predominantly aquatic habits, capable, however, of progression, doubtless with much labor, upon land. Its position among the Amphibia is not assured In the complete ossification of the vertebræ it has its nearest relationship among the Microsauria, the Lepospondyli of Zittel, in which group it was placed by Cope when he recognized the amphibian nature of the genus, and to which it has also been assigned by Broili and Jaekel. Furthermore, in the structure of the skull, notwithstanding its extraordinary shape, it offers no important differences from that group so far as is known; the epiotics are enormously developed, it is true, but the epiotic notch is still preserved on the side.

In the articulation of the ribs, however, there is a profound difference, one which seems to ally the type with the modern Urodeles, as Cope intimated in his early descriptions. The true microsaurians have single-headed ribs attached intercentrally, or at least the capitulum is always so attached — in *Diplocaulus* the elongated diapophyses arising from the arch, and the equally elongated parapophyses from the centrum near the middle anteroposteriorly. There is perhaps no more important ordinal character among the early air-breathing vertebrates than the mode of attachment of the ribs. No such difference as *Diplocaulus* presents is found anywhere among the members of the reptilian orders.

I by no means wish to suggest that *Diplocaulus* should be separated from the microsaurians as a distinct order, but that that group is entitled to a higher rank than that of a family I do believe. Furthermore, as I have said, *Crossotelos*, so far as the vertebræ are concerned, must be associated with *Diplocaulus*. If I am correct, however, in my recognition of the skull of this genus, it is of a widely different type from that of *Diplocaulus;* and the limb bones also, so far as I have determined them, are very different. The genus indeed represents a distinct family from Diplocaulidæ—the Crossotelidæ, further details of which I shall give in a future paper.

SOME NOTES ON THE OLYMPIC PENINSULA, WASHINGTON.

By ALBERT B. REAGAN, La Push, Wash.

INTRODUCTION AND ACKNOWLEDGMENTS.

THE field-work upon which this paper is based has been carried on as time would permit for the past four years, the most of the work being done during the summer months of each year. The type fossils collected are in the writer's collection at La Push, Wash., duplicates are to be found in the geological collections of the Leland Stanford Junior University and in the museum of the Kansas Academy of Science.

The Olympic peninsula is a very difficult region in which to do geological research work. There are but two wagon roads in the entire area west of Mount Olympus. One of these roads, aggregating some forty miles in total length, connects Port Angeles with Lake Crescent and Port Crescent, and the latter again with Lake Crescent; the other road extends from East Clallam, on the Strait of Juan de Fuca, south to La Push, of the Pacific front, a distance of about fifty miles. Trails extend along the beach of both ocean and strait. Trails also extend from West Clallam to Ozette lake and the Dickey lake country, and from the latter on to Quillayute Prairie. Another trail connects Forks with the Hoh country. A few short trails also branch off from the main trails here and there. These afford all the means of gaining access to the interior, except by canoe on the various streams; for off of the trails and roads the fallen timber, underbrush and ferns make the forest such a jungle in most places that one cannot travel half a mile an hour.